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14. ABSTRACT <p>Bottlenose dolphins (<i>Tursiops truncatus</i>) have an acute ability to use target echoes to judge attributes such as size, shape, and material composition. Most target recognition studies have focused on features associated with individual echoes as opposed to information conveyed across echo sequences (feature envelope of the multi-echo train). One feature of aspect-dependent targets is an amplitude modulation (AM) across the return echoes in the echo train created by relative movement of the target and dolphin. The current study examined whether dolphins could discriminate targets with different AM envelopes. "Electronic echoes" triggered by a dolphin's outgoing echolocation clicks were manipulated to create sinusoidal envelopes with varying AM rate and depth. Echo trains were equated for energy, requiring the dolphin to extract and retain information from multiple echoes in order to detect and report the presence of AM. The dolphin discriminated amplitude-modulated echo trains from those that were not modulated. AM depth thresholds were approximately 0.8 dB, similar to other published amplitude limens. Decreasing the rate of modulation from approximately 16 to 2 cycles per second did not affect the dolphin's AM depth sensitivity. The results support multiple-echo processing in bottlenose dolphin echolocation. This capability provides additional theoretical justification for exploring synthetic aperture sonar concepts in models of animal echolocation that potentially support theories postulating formation of images as an ultimate means for target identification.</p> <p>Published in <i>Journal of the Acoustical Society of America</i>, October 2002. Vol. 112, No. 4, pp. 1702-1708.</p>						
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Discrimination of amplitude-modulated synthetic echo trains by an echolocating bottlenose dolphin

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Bottlenose dolphins (*Tursiops truncatus*) have an acute ability to use target echoes to judge attributes such as size, shape, and material composition. Most target recognition studies have focused on features associated with individual echoes as opposed to information conveyed across echo sequences (feature envelope of the multi-echo train). One feature of aspect-dependent targets is an amplitude modulation (AM) across the return echoes in the echo train created by relative movement of the target and dolphin. The current study examined whether dolphins could discriminate targets with different AM envelopes. "Electronic echoes" triggered by a dolphin's outgoing echolocation clicks were manipulated to create sinusoidal envelopes with varying AM rate and depth. Echo trains were equated for energy, requiring the dolphin to extract and retain information from multiple echoes in order to detect and report the presence of AM. The dolphin discriminated amplitude-modulated echo trains from those that were not modulated. AM depth thresholds were approximately 0.8 dB, similar to other published amplitude limens. Decreasing the rate of modulation from approximately 16 to 2 cycles per second did not affect the dolphin's AM depth sensitivity. The results support multiple-echo processing in bottlenose dolphin echolocation. This capability provides additional theoretical justification for exploring synthetic aperture sonar concepts in models of animal echolocation that potentially support theories postulating formation of images as an ultimate means for target identification. © 2002 Acoustical Society of America. [DOI: 10.1121/1.1504856]

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I. INTRODUCTION

The basic requirement for any man-made or biological underwater sonar system is to detect a signal, usually an echo, in the surrounding noisy sea. For the dolphin, this detection is accomplished in part by extensively adapted auditory neural systems about which the functional capabilities are not yet fully understood. The exquisite biological sonar system of the bottlenose dolphin (*Tursiops truncatus*) is a prime example of evolutionary adaptation for use in shallow water, cluttered, high noise, and extremely reverberant environments such as bays, estuaries, and near-shore waterways. Although this capability has evolved over the past 50 million years, the discovery of dolphin echolocation is comparatively new, dating back to the late 1940s (Busnel and Fish, 1980). Since then, research conducted under rigorous experimental conditions has demonstrated that dolphins have an acute ability to judge from returning target echoes whether that target is hollow or solid, how thick it is, and to judge attributes such as size, shape, and material composition (Au,

1993; Busnel and Fish, 1980; Helweg *et al.*, 1996; Nachtigall and Moore, 1988; Thomas and Kastelein, 1990).

Although many previous studies have addressed the basic question of what acoustic features are used by the dolphin in biosonar target recognition, most have focused on features associated with *individual* echoes returning from ensounded targets. This approach disregards information that may be conveyed across dynamic or static features of echo sequences (echo train), or multi-echo integration. Floyd (1980) provided the first application of signal detection theory to multiple observations (Swets *et al.*, 1988) in dolphin echolocation. He provided three models of echo detection in noise that contrasted coherent summation, noncoherent summation, and independent evaluation processes. In contrast to Floyd's detection models, the current study examines whether dolphins are capable of using changes in echo amplitude over the course of multiple echoes (echo envelope) to discriminate targets.

Traditionally, the amplitude modulation (AM) of echo envelopes most often has been discussed with reference to the effects of insect wing beats on the envelope of individual bat echolocation calls (Busnel and Fish, 1980; Nachtigall and Moore, 1988). A bottlenose dolphin echolocation click is ba-

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sically too brief to sustain much AM, but the return echo contains multiple highlights. The energy contained in the highlights may be integrated, enhancing the dolphin's echo detection performance (Vel'min and Dubrovskiy, 1976; Moore *et al.*, 1984). In contrast, some information about object shape can be carried by the AM of an echo train, but discrimination of objects based on the amplitude envelope of the echo train has not been reported. Several theories include the assumption that dolphins are sensitive to systematic changes across multiple echoes. In a computational model of dolphin echo signal processing designed to account for the observation that dolphins usually emit multiple clicks during biosonar research tasks, combination, or fusion, of multiple echoes resulted in improved echo categorization (Moore *et al.*, 1991; Roitblat *et al.*, 1991). Altes *et al.* (1998, 2001) produced synthetic aperture sonarlike images by combining echoes from objects ensounded at multiple orientations with dolphin clicks, providing a theoretical foundation for speculation that dolphins form images of objects using information gathered through echolocation (Harley *et al.*, 1996; Herman *et al.*, 1998).

Multi-echo integration is analogous to the use of sequential aspect changes for discriminating between objects or identifying orientation of aspect-dependent objects. One acoustic feature of echoes from aspect-dependent targets is the AM of the return echoes in a train, which can be a function of the changing orientation of the target relative to the dolphin. Multi-echo integration capability would render a dolphin able to discriminate an amplitude-modulated echo train from one of constant amplitude, while total energy is held constant. Sensitivity to the AM of multiple echoes has not been directly measured, however. A previous study has shown an echolocating dolphin to be capable of detecting a 1-dB difference in target strength upon comparing return echoes from stationary targets (Evans, 1973). Physiological evidence from evoked-potential recording from inferior colliculus (Bullock *et al.*, 1968), and behavioral results from both free-field threshold tests of absolute hearing ability (Johnson, 1967) and interaural measures (Moore *et al.*, 1995), all have demonstrated sensitivity to amplitude changes as low as 1 dB. These results suggest that a dolphin capable of multi-echo integration may be similarly sensitive to the AM of echo sequences.

The current study was designed to test the hypothesis that echolocating dolphins can detect changes in amplitude of an envelope formed by multiple echoes and to examine limits of such ability. Testing was accomplished using electronic echoes generated interactively by computer as a dolphin emitted echolocation clicks. The use of electronic echoes permitted strict experimental control over the stimulus features available to the dolphin, since control of the features would not have been possible using physical targets. This is the first study of amplitude sensitivity in the "active" auditory system. From a biomimetic, signal processing standpoint, this work has application to understanding if and how one should go about "fusing" multi-aspect information.

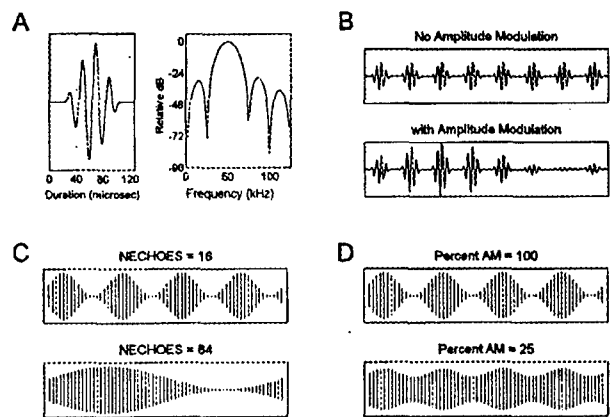


FIG. 1. (A) Enlargement of a single stimulus pulse (left) and its spectrum (right). (B) Examples of a GO and NO-GO stimulus used in the experiment. Each stimulus was comprised of multiple echoes over which amplitude was constant (NO-GO) or modulated (GO). (C) Comparison of two GO stimuli that have equal %AM, but differ in number of echoes (NECHOES=16 and 64 shown). The rate at which the envelope of the GO stimulus was modulated was a function of the number of echoes used to define it. Each vertical line represents a single synthetic echo. (D) Envelope contour was determined by % AM, the difference between echoes of highest and lowest amplitudes. The NECHOES is 16 in this portion of the figure.

II. METHODS

A. Subject

The subject of this study was a 17-year-old female bottlenose dolphin, "CAS." CAS was housed with two companion dolphins in enclosures located in San Diego Bay at the Space and Naval Warfare Systems Center facilities. Experimental sessions were conducted in an enclosure that was inaccessible to the other animals. The subject's hearing was recently evaluated as normal by a comprehensive audiometric assessment (Brill *et al.*, 2001).

B. Synthetic echo stimuli

Each trial consisted of a series of synthetic echoes triggered by the dolphin's outgoing echolocation clicks, with one synthetic echo generated per click emitted by the dolphin. In both AM and no-AM trial type conditions [Fig. 1(B)], individual echoes were triangle-windowed 50-kHz pulses, 128 μ s in duration. The stimuli were used to test specific experimental parameters and were not intended to mimic echoes from real objects in a naturalistic setting. The analytic waveform and spectrum are illustrated in Fig. 1(A). Digital waveforms were corrected for the transducer's measured transmit response prior to analog conversion. Calibration measurements confirmed good match between desired and analytic spectra.

Ambient noise in San Diego Bay was approximately 80 dB *re*: 1 μ Pa²/Hz above 1 kHz, so a consistent noise floor was created by the addition of 95 dB SPL of white noise to all synthetic echoes used in the experiment. The bandwidth for rms noise power was estimated using Q derived from critical band measures of the bottlenose dolphin receiver. Q was approximately 2.2 for signals with center frequency of 60 kHz (Au and Moore, 1990). The synthetic signals used in

this study had center frequency of 50 kHz, thus the 95 dB SPL white noise floor was set using an estimated bandwidth of approximately 22.72 kHz.

To prevent the dolphin from attempting to solve the discrimination using only the first synthetic echo of each trial, the starting phase of the AM sinusoid was randomized by drawing from a Gaussian distribution with mean of 90 (± 5) degrees. This manipulation equated the starting amplitude of the first echoes of the no-AM and AM echo trains.

Two aspects of the amplitude envelope modulation contour were varied in this study—depth of modulation and the rate at which the modulated contour changed. The depth of AM in the GO stimulus envelope was manipulated by varying notch depth, defined as %AM [Fig. 1(D)]. The amplitude of the NO-GO synthetic echo trains was constant, and GO synthetic echo amplitudes varied depending on %AM. The source level was held constant at 133 dB SPL *re*: 1 μ Pa for all NO-GO echoes, except during training. GO stimulus echo trains had equivalent source level on average, with individual echo levels ranging between 0 and 139 dB (depending on the %AM value) prior to the addition of white noise.

Assessment of CAS's sensitivity to AM as a function of time was examined by requiring the AM to cycle through a complete period over a predetermined number of echoes (NECHOES; 4, 8, 16, 32, or 64) [Fig. 1(C)]. Greater amplitude differences between successive echoes were therefore necessary at NECHOES=4 ($|\Delta\text{dB}|=0.32$; %AM=100) than at NECHOES=64 ($|\Delta\text{dB}|=0.02$; %AM=100). Thus, the highest AM rate was associated with NECHOES of 4, and the lowest with 64. Furthermore, AM envelopes were briefest for the NECHOES=4 condition and longest for NECHOES=64. Although echo presentation pace was partly determined by the animal since her clicks triggered synthetic echo delivery, the equipment was designed to simulate a 6-m range by limiting the interecho interval so that echoes could not be triggered any faster than 8 ms apart. Thus, at higher levels of NECHOES, the full range of AM information was delivered over a longer period due to the inter-echo interval restriction.

Percent AM can be equated with a minimum amplitude difference detectable by the dolphin. Total energy was held constant across the echo train, thus the dolphin could not simply solve the discrimination by cumulative energy differences that would otherwise emerge across the echo train. Two measures of %AM therefore could be derived—the amplitude difference between adjacent echoes (a pairwise comparison) or the overall amplitude difference (max-min echo amplitudes) (Fig. 2). The former relationship makes the fewest memory assumptions, assuming a sliding memory register only two echoes deep. The latter assumes a deeper memory register (fill the register then make the max versus min comparison). We converted %AM to minimum amplitude difference using the latter relationship, which provides the most conservative (less sensitive) estimate.

C. Apparatus

An electronic Synthetic Echo System (SES) was assembled for the purpose of detecting the dolphin's echolocation clicks and delivering the corresponding synthetic ech-

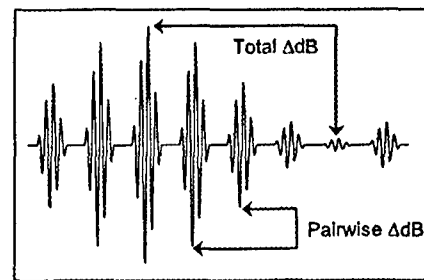


FIG. 2. Relationship between %AM of the echo train envelope and potential measures of amplitude limens.

oes. System onset, experimental variables (%AM, NECHOES), trial type (GO, NO-GO), and response logging were controlled using a LabView Virtual Instrument driver with a National Instruments PCI MIO-16E-1 multifunction board hosted on a Pentium PC. The digital synthetic echoes were combined with white noise, and the resultant signals stored to RAM prior to each trial.

An apparatus was constructed for animal and hydrophone placement during sessions. The subject's hoop station was situated 1.35 m below the water surface and 0.48 m away from an acoustically opaque shield. Shield removal indicated start-of-trial, and CAS's clicks were then detected by a Reson TC4013 omnidirectional broadband hydrophone located 0.64 m from her melon. The analog input data were bandpass filtered (3–300 kHz), amplified (54 dB of gain; Stanford Research Systems SR 560 filter/amplifier), and then passed to the multifunction board. Every emitted click exceeding 170 dB *re*: 1 μ Pa triggered the analog output of a synthetic echo by the SES. Analog echoes were filtered and amplified (10–200 kHz, 20 dB of gain) using a DL Electronics 4302 filter/amplifier, and projected by a second Reson TC4013 hydrophone located 1.35 m from CAS's melon. A 6.0-m range was simulated by inserting a delay of 8.0 ms between the triggering click and output of the echo, thereby providing a consistent focal point for the animal. Surface reflections were eliminated by a floating mat comprised of nylon bristles located at the surface between the dolphin and the Reson transducers. The system was calibrated by transmitting the synthetic echoes from the Reson TC4013 transducer and receiving them on a calibrated ITC 6030 omnidirectional hydrophone located at the dolphin's position in the hoop station.

D. Session procedure

Each trial began with the dolphin placing her rostrum on an inter-trial station located at the water surface, facing a trainer. Upon receipt of a hand cue from the trainer, CAS submerged and positioned her head in the test station hoop. The trainer raised the shield out of her echolocation pathway as a computer operator engaged the synthetic echo electronics. A 4.0-s trial period ensued, during which time the subject could echolocate *ad libitum*. A synthetic echo was produced for every click received. The subject was required to back out of the stationing hoop and touch a nearby paddle (GO response) to report an AM synthetic echo train and required to remain in the hoop for 4.0 s (NO-GO response) to report a

no-AM echo train. A miss was recorded if the animal performed a NO-GO response for the AM condition, and a false alarm recorded if a GO response was made to a no-AM stimulus. Correct responses were reinforced with a secondary (1-s 5-kHz tone) and a primary (approximately three fish) reinforcer. Incorrect responses were not reinforced. Trials were arranged in blocks of ten, with an equal number of GO and NO-GO trials presented per block. Trial type sequencing was determined by a Gellermann series (Gellermann, 1933) modified so that successive trials within a block were controlled (0.5 first order conditional probability of a GO trial following a NO-GO, or vice versa). Sessions began with an easily discriminable ten-trial block to assess subject motivation. The session was suspended temporarily if performance was below 80%. One data session was conducted per day.

E. Training and experimental phases

1. Training

In order to train CAS to perform the appropriate responses for both stimulus types, the stimuli were initially varied in both overall energy and envelope modulation. CAS was first exposed to the GO stimulus only (modulated envelope, %AM=100 and NECHOES=4) and learned to perform the appropriate corresponding paddle-press response (three to four sessions). During these sessions, on approximately half of the trials, no synthetic echoes were delivered and the NO-GO response was reinforced. Over the next 20 sessions, the NO-GO stimulus echoes (no-AM) were introduced at a source level of 118 dB SPL and increased by 3.0 dB every 10–50 trials until the total energy equaled that of the GO stimulus (133 dB SPL). Once signal energy was equated, envelope modulation alone provided the only feature upon which discrimination was possible. Successful completion of this phase of training established CAS's ability to discriminate between modulated and unmodulated echo trains and prepared her for tests in which the AM depth and rate were changed.

2. Threshold titration

All sessions in which %AM was systematically adjusted to measure CAS's threshold followed a titration method similar to the up/down staircase as reported by Moore and Schusterman (1987). Sessions began with the AM parameter held constant and at an easily discriminable level. If the initial ten-trial block was successful (performance $\geq 80\%$), %AM was then decreased in 2% increments for every GO stimulus trial until an incorrect response to a GO stimulus was given. Adjustments to %AM for all subsequent GO stimulus trials were then made in 1% increments. The %AM was increased after a miss and decreased after a correct GO response. Adjustments to %AM were never contingent on NO-GO stimulus trial responses. A reversal was defined as an instance in which the %AM adjustment changed directions (reversed), with the first reversal of every session occurring on the first incorrect GO stimulus trial. A session ended after ten reversals had been collected. The %AM

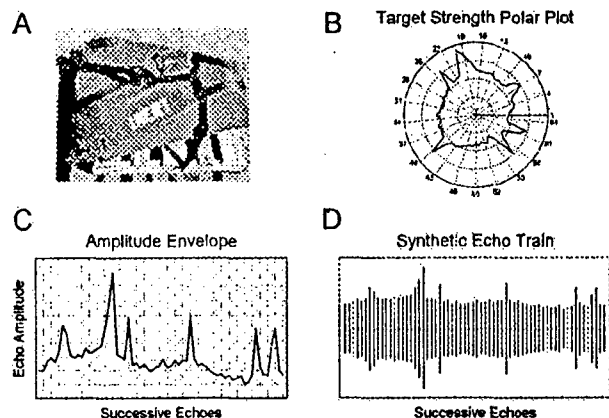


FIG. 3. Derivation of the amplitude envelope from the ROCKAN mine simulator. A photograph of the ROCKAN simulator on a palette is shown in (A), and (B) is the polar plot of the free-field target strength measured for the object (measured at the Applied Research Laboratory, University of Texas at Austin—Lake Travis test facility). (C) illustrates the amplitude profile when the polar data are unwrapped. (D) illustrates the amplitude variation in the synthetic echo train when the envelope is applied to a 64-echo train.

threshold estimate was defined as the mean of the %AM reversal values, which corresponds to a 50% correct discrimination performance.

3. Testing

Testing was conducted in four stages.

a. Stage 1: NECHOES. The first measure was a preliminary assessment of CAS's AM discrimination ability at all NECHOES levels. Only one level was utilized per session. With %AM held constant at 100, performance was bracketed in one to three 20-trial (approx.) sessions, first at NECHOES=8, followed by 16, 32, and lastly 64.

b. Stage 2: Percent AM. With NECHOES held constant at 8, %AM was titrated down to threshold level. Five sessions were conducted overall, the last two of which were ten-reversal threshold sessions. CAS's performance at "NECHOES" and "%AM" assessment phases provided estimates of her performance boundaries at these stages. Thus, detailed testing could be initiated using stimulus values closer to her estimated thresholds.

c. Stage 3: NECHOES & %AM. Systematic testing of CAS's discrimination ability of the depth and rate of an AM echo train was conducted whereby %AM was titrated at each NECHOES level in two threshold sessions. Sessions in which NECHOES=16 were conducted first, followed by sessions at 32, then 64. Bracketing threshold sessions (two to three) were conducted at each NECHOES level before experimental data was collected.

d. Stage 4: Envelope modulation. Five 40-trial sessions were performed in which the GO stimulus AM was derived using scaled acoustic backscatter from a ROCKAN mine simulator, an object roughly shaped like a triangular wedge [see Fig. 3(A)]. This phase investigated whether CAS was able to detect AM echo trains using the amplitude envelope from the mine simulator. NECHOES and %AM were held constant at 64 and 100, respectively. The polar plot of relative target strength from the real world object is presented in

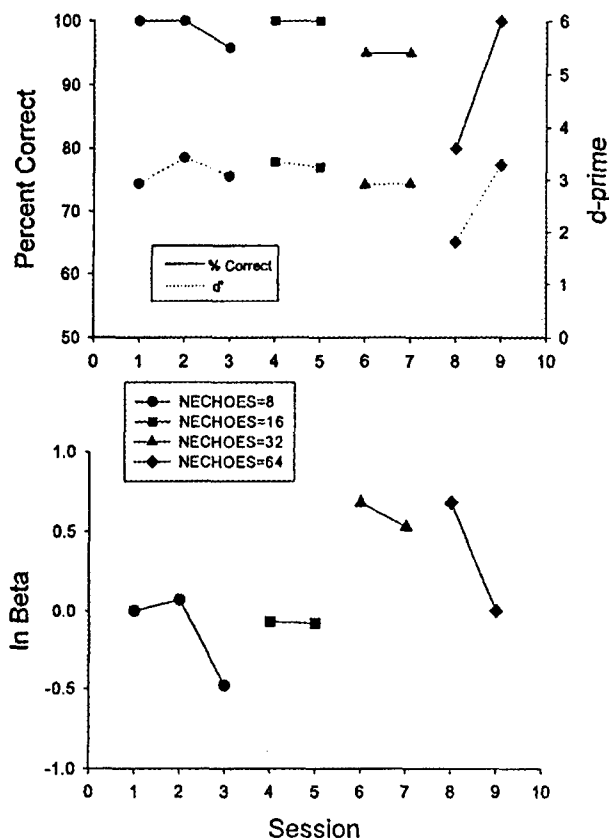


FIG. 4. Stage 1 preliminary AM rate assessment: Behavioral performance results at different AM rate levels (NECHOES=8, 16, 32, and 64) while %AM was held constant at 100 are shown. Percent correct performance (%) and sensitivity (d') results are presented in the top graph, and response bias [$\ln(\beta)$] in the bottom (20-trial sessions).

Fig. 3(B), and the 64-point extracted test envelope modulation function is presented in Figs. 3(C) and (D).

F. Data analysis

Behavioral results from stages 1 and 4 (NECHOES; envelope modulation) were evaluated using the theory of signal detection (TSD) (Green and Swets, 1988). Both the subject's signal detection sensitivity (d') and response bias (β), reported as $\ln(\beta)$, were computed in these instances since signal parameters (AM depth and rate) were not varied during a session. Results from stages 2 and 3 were evaluated by estimating thresholds using the mean of the titration reversals (50% correct discrimination performance).

III. RESULTS

A. Number of echoes (NECHOES)

Sessions in which NECHOES varied while %AM was held constant at 100 (Stage 1) are shown in Fig. 4. Percent correct performance and signal detection characteristics (d' ; β) are plotted as a function of NECHOES. CAS's ability to discriminate AM trials from no-AM trials remained at or above 80% correct for all levels of NECHOES. Choice performance and sensitivity (d') were equally strong at NECHOES=8, 16, and 32, but the increase in β at NECHOES=32 shows that CAS became conservative in her

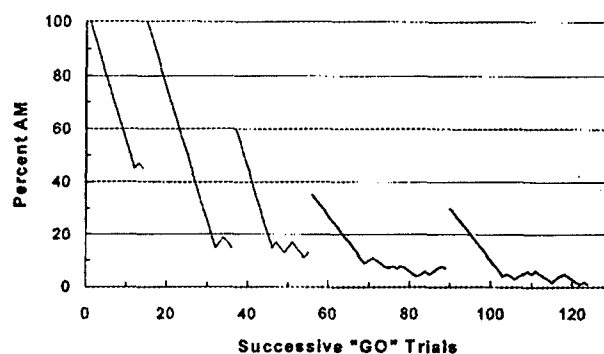


FIG. 5. Stage 2 initial %AM titration data: Percent AM values by trial during training sessions ($n=3$) and subsequent threshold estimates ($n=2$) (NECHOES=8 for all) are shown. Only AM trials (GO condition) are represented, and sessions are presented from left to right in the order they were conducted.

responding, possibly indicating a shift in her response strategy as the NECHOES were increased. CAS had poorer discrimination performance during the initial NECHOES=64 session, as evidenced by the low sensitivity value (d') and higher β . This performance decrement was resolved by the second session, suggesting a growing familiarization with the stimulus at NECHOES=64. The β values across sessions show a slight tendency toward more liberal responding in the subsequent sessions of each NECHOES level. Taken together, these results suggest that the subject tended to be conservative in her responding when first introduced to a new NECHOES level, but demonstrated a clear ability to discriminate the AM stimuli as NECHOES was manipulated.

B. Initial %AM titrations

Titration results of the first five sessions in which %AM varied and NECHOES were held constant at 8 (Stage 2) are presented in Fig. 5. All AM trials are shown, with reversals depicted by the point at which the line changes direction. These trials are represented graphically in the order they were conducted across the five sessions. The first three sessions clearly illustrate CAS's learning of the %AM manipulation task, with performance nearly asymptotic after session 3. In the first session, initial exposure to the test stimulus culminated in only three reversals with a mean of 45%AM. The two subsequent sessions consisted of two and five reversals, respectively, with an average value of 17%AM at both session's reversal points. Finally, two ten-reversal threshold sessions were conducted, yielding first a 7.3%AM threshold, then a 3.9% threshold. The subject's ability to discriminate %AM improved with each session, and performance reached asymptote by the fifth session. These results indicate that the subject was able to discriminate very small amplitude modulations at NECHOES=8.

C. NECHOES and %AM

Threshold estimates for the %AM obtained at NECHOES=8, 16, 32, and 64 are shown in Fig. 6. The two sessions reported for NECHOES=8 are the same two threshold sessions describe in the previous section (initial %AM titrations). Thresholds were calculated using the 50% correct

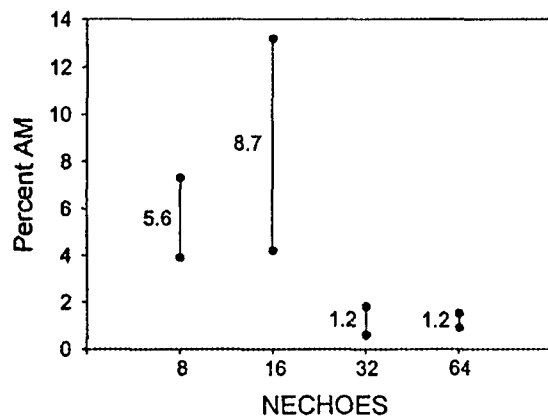


FIG. 6. Stage 3 threshold testing: Behavioral performance results on two %AM titration sessions (threshold estimates) at each AM rate (NECHOES=8, 16, 32, and 64) are shown. Thresholds are denoted by single points, with a line added to depict the range. The means of every threshold pair are adjacent to each line. NECHOES=8 data were taken from the two ten-reversal threshold sessions conducted in stage 2.

discrimination performance (mean reversal value for each session), and false alarm rates ranged from 0.01 to 0.40, with a mean value of 0.25. For each NECHOES level, two ten-reversal thresholds are plotted and the corresponding mean value noted. The animal's overall performance shows improvement in discrimination ability across sessions irrespective of the increase in NECHOES.

D. Object envelope simulation

Five 40-trial, minelike envelope discrimination sessions were conducted in which NECHOES=64 and %AM=100 for all sessions. Testing discrimination ability as opposed to measuring thresholds of that ability was the goal of this phase. The subject performed at 97% correct on four of the sessions and 100% on the other. The mean d' was 3.66 (sd=0.14) and mean $\ln \beta$ equaled 0.24 (sd=0.48), indicating that her discrimination performance was stable across sessions (Table I). These results show that CAS had little difficulty discriminating the irregular AM envelope associated with the minelike object.

IV. DISCUSSION

The major finding of this study was that an echolocating dolphin was able to discriminate amplitude-modulated (AM) echo trains from those that were not modulated, and that ability persisted as both rate and depth of AM were manipulated. Discrimination accuracy was maintained as rate of envelope modulation decreased. As AM depth was reduced,

discrimination thresholds stayed consistently low, indicating a high degree of sensitivity to changes in the amplitude envelope of an echo train. Furthermore, decreasing the rate of modulation did not adversely affect this sensitivity to reductions in AM depth. These results provide data in support of the hypothesis that dolphins may recognize targets using features compiled across multiple echoes (envelope of an echo train). Further empirical support was offered by the finding that when successive echo amplitudes rose and fell irregularly, as real-world objects do, the echo train was easily distinguishable from a non-modulating echo train, as evidenced by a nearly perfect discrimination performance by the dolphin.

The average of all AM thresholds was approximately 4.2% AM, which corresponds to an 0.8-dB total variation in amplitude (maximum - minimum) across the sequence of echoes. The largest difference between any two successive echoes at the slowest modulation rate (NECHOES=64) was approximately 0.02 dB. It does not seem likely, therefore, that the dolphin could have used this two-echo amplitude difference (cf. Dubrovskiy *et al.*, 1978) to accomplish AM discrimination. Past research has demonstrated amplitude discrimination limens no lower than about 1 dB (Bullock *et al.*, 1968; Evans, 1973; Johnson, 1967; Moore *et al.*, 1995). The %AM threshold of 4.2% (0.8 dB) of this study is consistent with the other amplitude discrimination limens, supporting speculation that the dolphin's echo memory register is more than two echoes deep and may be substantially deeper, given CAS's high performance with 64-echo trains.

We can speculate about the amplitude modulation rates experienced by the dolphin in this study. The minimum inter-echo interval was 8 ms, corresponding to a maximum rate of 125 echoes per second. At NECHOES=8, a full AM cycle occurred in approximately 64 ms, or an AM rate of approximately 15.6 echoes per second. At NECHOES=64, a full AM cycle occurred in 512 ms, or an AM rate of approximately 1.9 echoes per second. These rates are the maximum that the dolphin could have experienced (see Murchison, 1980; Penner, 1988).

The dolphin's ability to discriminate amplitude-modulated echo trains is not explained by the energy integration mechanism that underlies detection of single echoes in noise (Moore *et al.*, 1984; Vel'min and Dubrovskiy, 1976; Au *et al.*, 1988). Within echoes, inter-highlight intervals tend to be measured in tens of microseconds. In contrast, the synthetic echoes used in this study were separated by a minimum of 8 ms, which is orders of magnitude greater than the 265- μ s energy integration window (Moore *et al.*, 1984; Vel'min and Dubrovskiy, 1976; Au *et al.*, 1988). Thus, any information used by the animal to distinguish one echo train type from another was based solely on an ability to extract and retain information from successive echoes in order to arrive at a decision regarding the varying amplitude characteristics of the train. The ability to garner information from the combination of multiple echoes—in addition to individual within-echo highlights—would serve to heighten detection and classification performance for objects encountered in the environment, as computational models have demonstrated (Floyd, 1980; Moore *et al.*, 1991; Roitblat

TABLE I. Percent correct performance and signal detection characteristics for each envelope simulation session (Stage 4, $n=20$ trials per session).

Session	% Correct	d'	$\ln(\beta)$
1	100	3.91	0.02
2	97	3.60	0.57
3	97	3.60	0.57
4	97	3.60	0.57
5	97	3.57	-0.51

et al., 1991, 1993). The results provide theoretical justification for exploring the application of synthetic aperture sonar concepts in multi-echo models of animal echolocation (e.g., Altes *et al.*, 1998, 2001), which has ramifications for mental imagery theories that postulate formation of object images as an ultimate means for their identification (Harley *et al.*, 1996; Herman *et al.*, 1998). Future studies on dolphin biosonar capabilities should therefore examine aspects of information processing from complex echo trains as well as individual echoes.

Because echo trains are comprised of multiple echoes, the dolphin necessarily received more than one echo per trial. Prior research has shown that stimulus detectability can be enhanced in humans when multiple observations are allowed (see Floyd, 1980; Swets *et al.*, 1988; Green and Swets, 1988 for review). Those studies were designed to elucidate the possible mechanisms by which detection occurs as opposed to measuring the degree of detection enhancement. The classical interpretation of multiple observations and their implication on results of the current study are not considered applicable as this study did not utilize noise-only trials (no signal present) as a detection task would require, and no attempt was made to address the theory *a priori*. The potential contribution of this phenomenon to multiple echo integration capabilities in the dolphin could provide an interesting basis for further study.

In conclusion, the results reported here provide additional support for multiple-echo processing in bottlenose dolphin echolocation, and this, in turn, provides additional theoretical justification for exploring the application of synthetic aperture sonar concepts in models of animal echolocation. Future studies should seek to provide explicit evidence of multi-echo fusion, and to test for coherent echo integration processes that underlie algorithmic-based synthetic aperture sonar imaging processing use in traditional signal processing approaches.

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